

MANAGING LEAF AREA FOR MAXIMUM VOLUME PRODUCTION IN A LOBLOLLY PINE PLANTATION¹

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Abstract—To manage loblolly pine (*Pinus taeda* L.) stands for maximum volume growth, the relationships between volume growth and leaf area at the tree and stand level under different cultural practices (thinning and fertilization) were examined. Forty-eight trees were harvested in 1995, six years after treatment, for individual tree measurements, and 336 standing trees were used for stand measurements each year from 1991 to 1994. Thinning significantly increased annual ring width, tree leaf area, and tree volume growth during the six years following treatment, but reduced stand leaf area index and stand volume growth. Fertilization increased leaf area and volume growth at both the tree and the stand level, but significant tree level effects were only apparent during the first three years following treatment. The combination of thinning and fertilization was the optimum overall treatment. The relationship between volume growth and leaf area was linear and positive at the both of tree and stand level across treatments.

INTRODUCTION

Studies of leaf area and growth dynamics of loblolly pine stands in response to silvicultural practices are currently in progress as part of the USDA Forest Service, Southern Global Change Program. Leaf area is a key measurement variable in ecophysiology studies of both individual trees and forest stands, because it reflects the amounts of energy and material exchange between the forest canopy and the atmosphere. The leaf area of tree crowns and stands has a direct effect on photosynthetic capacity by affecting the surface area for carbon fixation, and an indirect effect on photosynthetic capacity by influencing the radiation, temperature, water vapor, wind, and carbon exchange within the canopy (Drew and Running 1975, Gholz and others 1991). Numerous studies have established a positive relationship between leaf area and forest productivity (Brix 1983, Shelburne and others 1993, Vose and Allen 1988). Silvicultural practices such as thinning and fertilization may increase leaf area, above-ground tree growth, and root growth in many conifers (Brix 1981, Dougherty and others 1995, Haywood 1994, Sword and others 1996 and 1998, Vose and Allen 1988). Brix (1981) examined the effects of thinning and fertilization on annual leaf biomass and total leaf biomass per tree in Douglas-fir. He found that thinning and fertilization increased both annual leaf biomass and total leaf biomass. Increases in annual leaf biomass peaked 2-3 years after fertilization, while the greatest differences in total leaf biomass were not found until 4-7 years after fertilization alone. Short-term fertilization responses in loblolly pine leaf area have also been reported (Gillespie and others 1994, Vose 1988). Vose and Allen (1988) found that fertilization increased the leaf area index (LAI) of loblolly stands 2 years after treatment in nutrient-limited stands and that LAI varied with stand density. Stemwood volume growth was positively and linearly related to LAI across treatments and stands. However, the long-term effects of thinning and fertilization on loblolly pine leaf area and the relationship between leaf area and volume growth at tree and stand levels have not been reported. The objectives of this study were to (1) identify impacts of thinning and fertilization on tree volume growth; (2) assess the cultural practice effects

on leaf area of individual trees and stands; and (3) determine the relationship between leaf area and volume growth.

MATERIALS AND METHODS

Study Site

The loblolly pine (*Pinus taeda* L.) plantation in this study is located on the Palustris Experimental Forest in central Louisiana (31°07'N, 93°17'W). It was established in May 1981 when 14-week-old container-grown loblolly pine seedlings were planted at a spacing of 1.83 m by 1.83 m (2990 trees per ha). Twelve research plots, uniform in terms of tree size and spacing, were established within the plantation in the fall of 1988. Each plot was 23.8 m by 23.8 m (0.06 ha) and consisted of 13 rows of 13 trees. Two levels each of thinning and fertilization treatments were randomly assigned to 12 plots in a two by two factorial design resulting in four treatment combinations (thinned-fertilized, thinned-unfertilized, unthinned-fertilized, and unthinned-unfertilized) with three replications of each. On the thinned plots, 75 percent of the trees were removed in November 1988 by harvesting every other row of trees and every other tree in the remaining rows to produce a density of 731 trees per hectare. On the fertilized plots, diammonium phosphate at 744 kg per hectare (150 kg P + 134 kg N ha⁻¹) was broadcast in April 1989. The soil is a Beauregard silt loam (fine-silty, siliceous, thermic, Plinthic Paleudults). Soil drainage was adequate and slope was sufficient to prevent water from standing on the site (Haywood 1994).

Sampling and Measurements

Individual tree measurements—In early spring 1995, 48 trees were harvested from 12 plots (two dominant or codominant trees and two intermediate trees (lower in basal area) from each plot). Immediately after felling each sample tree, the height, live crown length and diameter at breast height (d.b.h.) were measured. Three disks were cut from each tree (one at breast height, one at the base of the live crown and one at the middle of the crown). The disks were placed in plastic bags, taken to the laboratory, and placed in cold storage until they were analyzed. The ring width and

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inside bark diameter for each year between 1988 to 1994 were measured to the nearest 0.1 mm in two vertical directions on the disk and then averaged.

Specific leaf area (projected leaf area per unit dry weight) was calculated from 96 sample shoots per treatment combination (Yu, 1996). Projected leaf area was measured to 0.01 cm² using a LI-3000 Leaf Area Meter (LI-COR Inc., Lincoln, NE USA). Needles of each shoot were oven-dried (60 °C) to a constant mass and weighed to 0.01 g. Mean tree projected leaf area was calculated based on needlefall dry weight, specific leaf area, and number of trees per plot.

Tree heights in the previous years were predicted from d.b.h. using the following equation:

$$\ln(H) = a_0 + a_1(1/D) \quad (1)$$

where H = total height, D = diameter at breast height, and a_0 , a_1 = coefficients. Tree volumes in each year were calculated separately for thinned and unthinned treatments based on Baldwin and Feduccia's volume equations (1987).

Stand measurements—The measurement plot was the interior portion of each treatment plot originally occupied by the central 7 rows of 7 trees each (0.015 ha). A total of 336 trees from the measurement plots were used to assess d.b.h. and 144 of these trees were used to measure total tree heights at the end of each growing season from 1991 through 1994. Stand volumes for each treatment and each year were obtained by summing tree volumes and expanding to a per hectare basis. Needlefall was collected, oven-dried (60 °C) to a constant mass, and weighed each week from four litterfall traps per plot (i.e. 12 traps per treatment combination) in 1993, 1994, 1995, and 1996. Each trap was 0.92 m². Litterfall dry weights were expanded to the plot level. Total leaf area per year and plot was estimated based on specific leaf area and two years of needlefall dry weights per plot (needlefall per year was summed from April to the following March) (Dougherty and others 1995, Vose and Allen 1988). Leaf area index was calculated from total leaf area per plot divided by plot ground area.

Statistical Analysis

The statistical significance of the thinning and fertilization main effects and the thinning by fertilization interaction effect was determined using analysis of variance (Statistical Analysis System, SAS V 6.12, SAS Institute Inc., Cray, NC, USA). Treatment effects on d.b.h., tree volume, stand volume, leaf area, and leaf area index in different years were analyzed by a two by two factorial in a completely random design. Treatment effects and their interaction with year on annual ring width, annual increment for diameter, tree height, tree volume, and stand volume were determined by a two by two factorial repeated measurements. Main and interaction effects were tested for statistical significance at the 0.1 probability level due to the low number of sample trees and large natural variation in forests. If the interaction of thinning by fertilization was significant, the simple effects were tested (Stehman and Meredith 1995) using adjusted Tukey test (Geaghan, J.P., personal communication, Department of Experimental Statistics, Louisiana State University).

RESULTS AND DISCUSSION

Individual Tree Level

Thinning and fertilization significantly increased d.b.h. (fig. 1A). The effects of thinning or fertilization on annual ring width significantly interacted with year. In 1988 before treatment, annual ring width was uniform. After treatment beginning in 1989 and continuing through 1994, thinning significantly increased annual ring width by 113, 191, 236, 145, 165, and 107 percent by year, respectively, compared to the unthinned treatment (fig. 1B). Fertilization significantly interacted with thinning during the first two years after treatment (table 1). Fertilization increased annual ring widths by 36 and 50 percent within the thinned plots in 1989 and 1990, but had no significant effect on the unthinned plot tree ring widths. In 1991, fertilization increased annual ring width by 35 percent. After 1992, the fourth year after treatment, fertilization effects on annual ring width were not significant. Annual ring width on the unthinned plots decreased after 1988 (fig. 1B), which indicated that crown closure occurred approximately 7-8 years after plantation establishment.

Tree height growth was significantly increased by fertilization ($P=0.0421$) but was reduced by thinning ($P=0.0001$). Mean tree height in 1994 was 14.99 m, 13.85 m, 15.24 m, and 14.18 m for the thinned-fertilized, thinned-unfertilized, unthinned-fertilized, and unthinned-unfertilized treatments, respectively. Tree height growth was immediately affected by the thinning treatment. However, fertilizer effects on height growth were delayed until the second year after treatment (Haywood, 1994).

Tree volume and tree volume growth were increased by thinning (fig. 1C and 1D). On the thinned plots, mean tree volume growth varied from 116 to 315 percent greater than in the unthinned plots over the period from 1989 to 1994. Fertilization significantly increased mean tree volume growth from 30 to 45 percent during the first three years after treatment. After 1991, fertilization effects decreased, and no significant differences between the fertilized and unfertilized treatments were found (table 1). These results are similar to those of Brix (1983). He found that thinning and fertilization increased individual tree annual stemwood growth in the first three to four years and then the effect of the fertilized treatment decreased.

Tree projected leaf area was not significantly different within treatments between 1993 and 1994. Interaction of thinning and fertilization did not significantly affect tree leaf area during this period. The trend in tree leaf area across treatments is shown in Figure 2. Thinning increased tree leaf area by 123 percent ($P=0.0001$), but fertilization had no significant effect on leaf area ($P=0.1134$) in 1994, 6 years after treatment (fig. 3). Brix (1981) reported that fertilization alone had little or no significant effect on foliage biomass 4 or 5 years after treatment, but the combination of thinning and fertilization increased foliage biomass per tree by 271 percent 7 years after treatment in a Douglas-fir stand. The difference between his results and ours related to the interaction effects of thinning by fertilization could be attributed to difference among tree species. Loblolly pine needles remain on the trees for about two years, while Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) needles are retained for 5-8 years. Thinning increased tree leaf area mainly by improving light transmission to the lower crown.

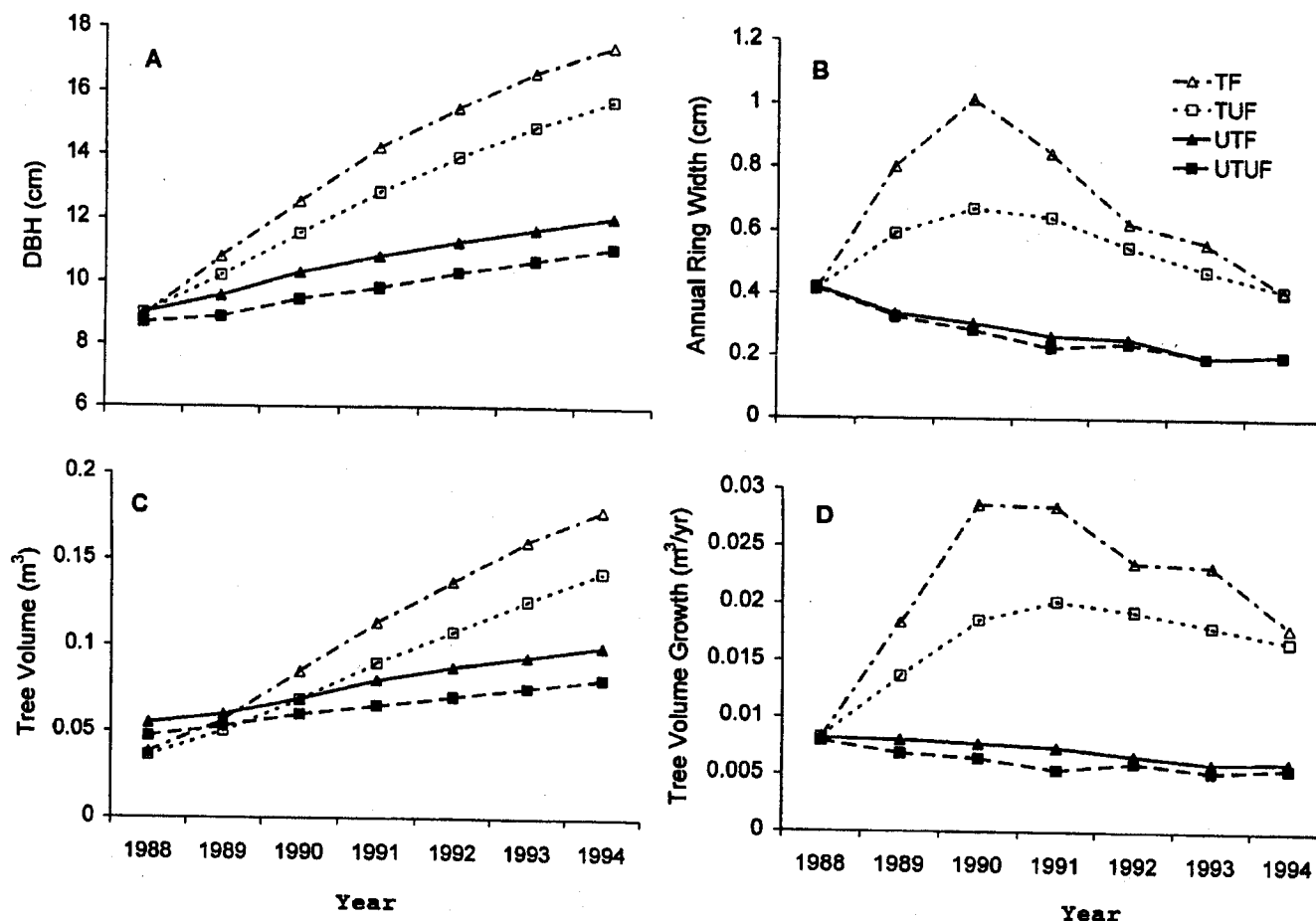


Figure 1—Mean diameter at breast height (d.b.h.) (A), annual ring width (B), tree volume (C), and annual tree volume growth (D) during 1988 (pre-treatment) through 1994 (TF = Thinned × Fertilized, TUF = Thinned × Unfertilized, UTF = Unthinned × Fertilized, UTUF = Unthinned × Unfertilized).

More light increased photosynthesis and led to more shoots per branch, branches per whorl, and whorls per tree after the thinning treatment (Ginn 1989, Gillespie and others 1994, Yu 1996).

Tree leaf area was linearly and positively related to volume growth ($R^2=0.84$) across treatments. When light and nutrient availability were increased, tree leaf area and volume growth were greater. Therefore, volume growth was the greatest on the thinned-fertilized treatment (fig. 4). Improved light availability on the thinned plots was associated with significant increases in shoot elongation and branch leaf area in the lower crown (Ginn 1989, Gravatt and others 1997, Tang and others 1999, Yu 1996) and stimulated early seasonal root growth (Sword and others 1998). Fertilization increased fascicle needle length and leaf area in the upper crown but not in the lower crown (Tang and others 1999, Yu 1996). In the thinned-unfertilized treatment tree leaf area and tree volume growth were less than those in the thinned-fertilized treatment. The lowest tree leaf area and tree volume growth occurred in the unthinned-unfertilized treatment. This response was likely due to nutrient deficiency and low light levels.

Stand Level

Small tree size at the time of thinning meant that the thinned trees were non-merchantable. Therefore, the volume of the thinned tree was not included in the stand volume data presented. Thinning and fertilization significantly affected residual stand volume. Fertilization increased stand volume on both the thinned and the unthinned plots (fig. 5A). In contrast, thinning resulted in less stand volume because 75 percent of the trees were harvested at the time of thinning. In 1992, the fertilized treatment significantly increased stand volume growth by 37 percent ($P=0.0075$), and the thinned treatment decreased stand volume growth by 40 percent ($P=0.0005$). As the period after tree removal increased, the negative effects on stand volume growth in the thinned treatment became less. The thinned treatment had only 31 percent ($P=0.0046$) and 29 percent ($P=0.0146$) lower stand volume growth in 1993 and 1994, respectively, than those in the unthinned treatment. In 1993, fertilized treatment had 41 percent ($P=0.0067$) greater stand volume growth than the unfertilized treatment. When treatments were combined as on the thinned-fertilized plots, stand volume growth was similar to the unthinned-unfertilized treatment (fig. 5B). Thus the fertilization compensated for the loss of stand volume

Table 1—Statistical summary (Probability >F) of treatment effects on ring width (cm), annual diameter growth (cm/yr) at breast height, tree volume growth (m³/yr)

Variable	Thinning	Fertilization	Thinning × fertilization
1988 (pre-treatment)			
Ring width	0.9156	0.9675	0.9935
Diameter growth	.9035	.9628	.9126
Tree volume growth	.6805	.4643	.5379
1989			
Ring width	.0001	.0008	.0007
Diameter growth	.0001	.3048	.0335
Tree volume growth	.0001	.0473	.2270
1990			
Ring width	.0001	.0114	.0159
Diameter growth	.0001	.0239	.0346
Tree volume growth	.0001	.0427	.0116
1991			
Ring width	.0001	.0288	.3216
Diameter growth	.0001	.0303	.3790
Tree volume growth	.0001	.0401	.3232
1992			
Ring width	.0003	.6202	.4567
Diameter growth	.0001	.5707	.3946
Tree volume growth	.0001	.3256	.4644
1993			
Ring width	.0001	.6425	.3511
Diameter growth	.0001	.3715	.3803
Tree volume growth	.0001	.2388	.3751
1994			
Ring width	.0001	.7831	.8839
Diameter growth	.0001	.8488	.9196
Tree volume growth	.0001	.6566	.8586

caused by thinning. The thinned-fertilized treatment was the optimum silvicultural practice for enhancing tree volume growth and potential productivity. Even though thinning reduced the number of trees per hectare remaining, trees on the thinned-fertilized treatment used the fertilizer to increase stand volume growth. Six years following treatment, although tree volume growth was no longer significantly affected by fertilization, stand volume growth continued to be significantly increased (30 percent, $P=0.0619$) by fertilization. A fertilization-induced increase in stand volume

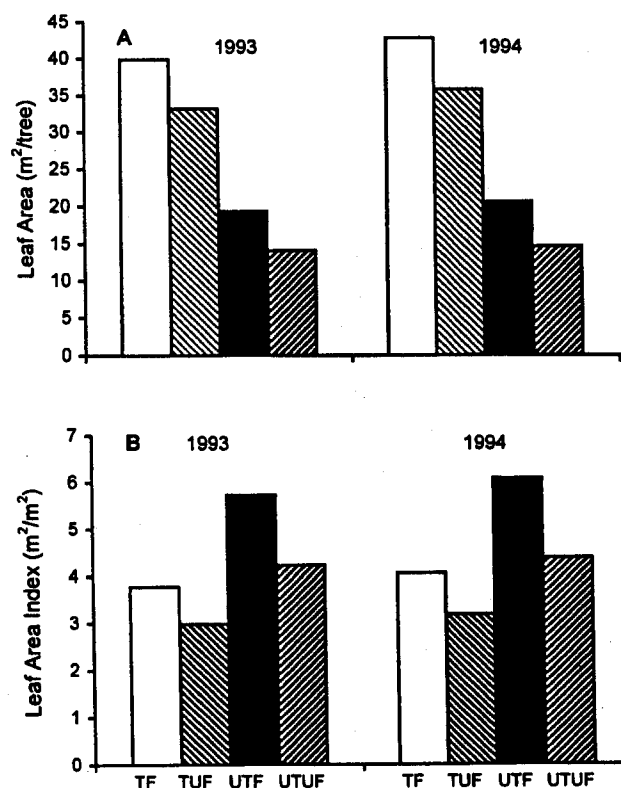


Figure 2—Mean tree leaf area (A) and stand leaf area index (B) in 1993 and 1994 (TF = Thinned × Fertilized, TUF = Thinned × Unfertilized, UTF = Unthinned × Fertilized, UTUF = Unthinned × Unfertilized).

growth was also reported by Vose and Allen (1988) and Albaugh and others (1998).

LAI (projected leaf area index) differences among treatments were similar in 1993 and 1994 (fig. 2B). Thinning and fertilization had a slight but not significant interaction effect on LAI ($P=0.1247$). The largest LAI occurred in the unthinned-fertilized treatment while the thinned-unfertilized treatment had the smallest LAI. Even though the thinned treatment had fewer trees than the unthinned treatment, the LAI in the thinned-fertilized treatment was similar to the LAI in the unthinned-unfertilized treatment. The similar LAI values indicate that fertilization stimulated leaf expansion and development, which compensated for fewer trees and thus helped recapture solar radiation and stand volume growth lost by thinning. In 1994, the fertilized treatment significantly increased LAI by 34 percent (fig. 3B). However, the thinned treatment had an overall negative effect on LAI, reducing LAI by 31 percent. The results from our study are similar to those from previous studies. Binkley and Reid (1984) reported that in a 53-year-old Douglas-fir plantation, fertilization increased stand leaf area and stem growth per hectare, and thinning reduced stand leaf area but increased stem growth per leaf area resulting in little difference in stem growth per hectare over a 5-year measurement period 13 to 18 years after treatment. Albaugh and others (1998) stated that fertilization increased LAI during a 4-year period after treatment in an 8-year-old loblolly pine stand.

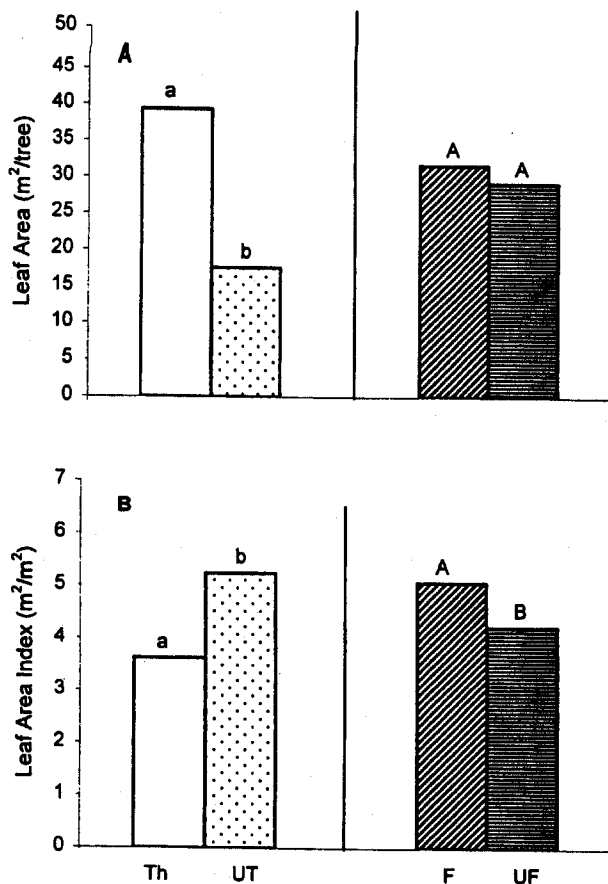


Figure 3—Thinning and fertilization main effects on mean tree leaf area (A) and stand leaf area index (B) in 1994. Different lower case letters indicates a significant difference between thinned and unthinned treatment, and different upper case letters indicates a significant difference between the fertilized and unfertilized treatments (Th = Thinned, UT = Unthinned, F = Fertilized, UF = Unfertilized).

Vose and Allen (1988) found that fertilization increased LAI of loblolly pine 2 years after treatment and LAI varied with stand density. They reported that stemwood volume growth was positively and linearly related to LAI across treatments and stands. In our study, LAI was also linearly correlated to stand volume growth across treatments ($R^2=0.78$). The unthinned-fertilized treatment had the largest LAI and also had the highest stand volume growth (fig. 4B). In contrast, the thinned-unfertilized treatment had the smallest LAI and the lowest stand volume growth. The thinned-fertilized treatment improved nutrient availability, and therefore increased both LAI and stand volume growth compared to the thinned-unfertilized treatment. A strong linear relationship between LAI and stand volume growth has also been demonstrated in other studies (Albaugh and others 1998, Binkley and Reid 1984).

SUMMARY

Thinning and fertilization are very useful silvicultural treatments. Thinning significantly increased tree leaf area and volume growth, but had negative effects on leaf area index and stand volume growth. These negative effects become less 4 years after treatments on the plots that were

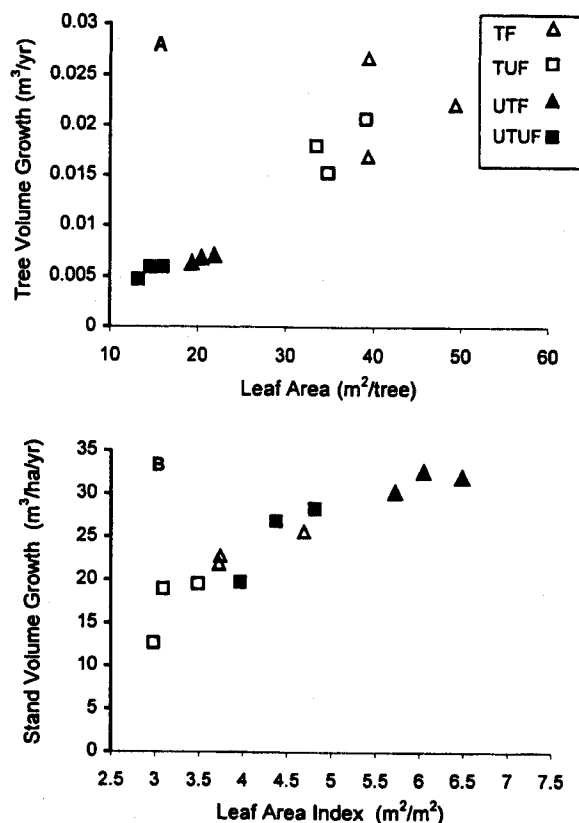


Figure 4—Relationship between annual tree volume growth and leaf area per tree (A) and annual stand volume growth and stand leaf area index (B) in 1994 (TF = Thinned × Fertilized, TUF = Thinned × Unfertilized, UTF = Unthinned × Fertilized, UTUF = Unthinned × Unfertilized).

fertilized at the time of thinning. Fertilization increased leaf area and volume growth at both the tree and stand level, especially during the first three years following treatment. There were linear and positive correlations between leaf area and volume growth at both the tree and stand levels. The combination of thinning and fertilization was an optimum silvicultural practice for sawtimber production on our study site. However, the choice of cultural treatment for managers depends on product market (fiber vs. sawtimber) and potential interaction between cultural practices and environment.

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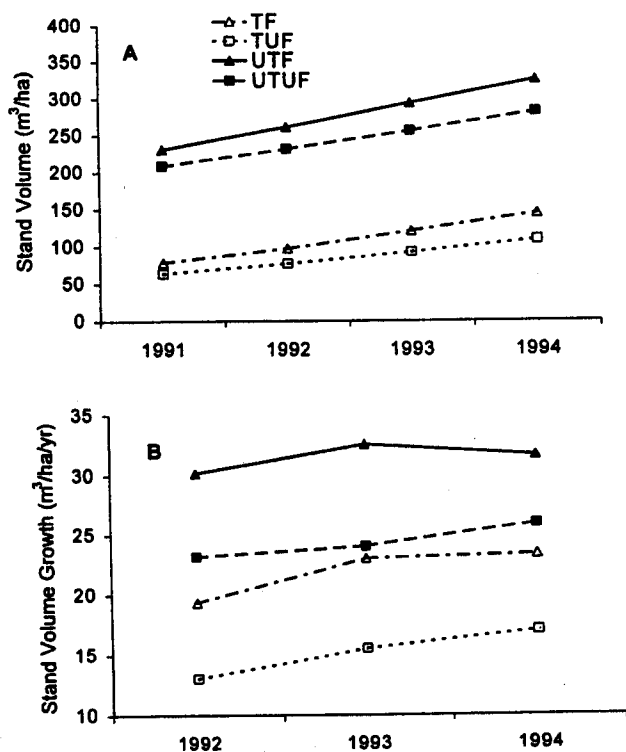


Figure 5—Mean stand volume for 1991 through 1994 (A) and annual stand volume growth for 1992 through 1994 (B) (TF = Thinned × Fertilized, TUF = Thinned × Unfertilized, UTF = Unthinned × Fertilized, UTUF = Unthinned × Unfertilized).

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